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Taxonomic Uncertainty, the Biological Species Concept, and the Nearctic Butterflies: a Reappraisal after Twenty Years

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Abstract. In 1961 Paul Ehrlich surveyed the Nearctic butterfly fauna in order to demonstrate that the biological species concept had "outlived its usefulness." A reappraisal of two genera, *Lethe* and *Pieris (sens. lat.)*, after twenty years leads to the conclusion that the biological species concept is still very useful in both systematics and evolutionary biology.

> The true understanding of the Atus of Tahuti, or Tarot Trumps, also awaits full understanding. I have satisfied myself that these twenty-two cards compose a complete system of hieroglyphs representing the total energies of the Universe. In the case of some cards, I have succeeded in restoring the original form and giving a complete account of their meaning. Others, however, I understand imperfectly, and of some few I have at present no more than a general idea.
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> *The Confessions of Aleister Crowley.*

Twenty years ago Paul Ehrlich asked himself "Has the biological species concept outlived its usefulness?" and answered "Yes." He bolstered his argument with a breakdown of the genera of Nearctic butterflies (Ehrlich, 1961), according to the purported ease with which distinct species could be recognized in them. Finding that a majority of the Nearctic genera included at least some ambiguous cases, he concluded that "at least at the present level of knowledge, the prevalence of the clearly defined species is a myth. . .the very nature of the biological species definition makes its use impossible in practice." This was strong language in 1961; it still is. It was echoed in a powerfully-argued paper in *American Naturalist* by Sokal and Crovello (1970). They did not use or cite Ehrlich's butterfly survey, but their conclusions were the same: the biological species concept (BSC) was unnecessary for practical taxonomy, neither necessary nor especially useful for evolutionary taxonomy, and neither an unique nor an heuristic concept necessary for generating hypotheses in evolutionary theory.

Ehrlich, Holm, and Parnell (1974) resurrected Ehrlich's study in the concluding, philosophical chapter of their undergraduate textbook, *The Process of Evolution*. By 1974 the debate between "evolutionary" taxonomists and pheneticists had become rather stale, but Ehrlich *et al.* did not relent on the "big" issues. If the phenetic perspective were to prevail, the BSC—with its presumption that phylogeny could be inferred at all—had to go. Despite persuasive rhetoric, it has not. It is interesting to contemplate the reasons for its persistence: mere inertia, or did the BSC really have something useful to offer?

As an evolutionist who works on butterflies and has to commit taxonomy from time to time, I found myself wondering just what, if anything, Ehrlich's 1961 survey had told us about the "species problem." It occurred to me that some kind of re-examination of his groups of genera after 20 years, with an eye to how the passage of time had affected our perceptions of species, might provide some inferences concerning the "usefulness" of the BSC, and the way we actually do use it, if we do.

My first impulse was to go through the lists, genus by genus, examining revisionary work done since 1961 to see whether ambiguous relationships had been clarified. I quickly gave up this idea. Such a genus-by-genus re-evaluation would have to be done by Ehrlich, not me, since his criteria for grouping the genera were of necessity vaguely defined. Even if I could reconstruct them, I doubt that I could interpret the changes fairly since I had disagreed in 1961 with the placement of perhaps a third of the genera. (There is also the peculiar problem that since 1961 a wave of splitting by butterfly taxonomists has so fragmented most of the genera that a newcomer to the field would be baffled by Ehrlich's lists.) But there is a more serious objection to this procedure: what would one learn from it? At the end of the exercise it might be possible to say that our wisdom regarding species increased by some quantity x, per year; one might even extrapolate to predict how long it would take to finish off the systematics of the Nearctic butterflies altogether. This is absurd, and its absurdity should become even clearer later in this paper.

Two Case Histories

A more fruitful approach, I decided, would be to examine a couple of genera I know well, having worked on them—*Lethe* and *Pieris*. Both of them must be reclassified in the Ehrlich scheme under any reasonable man's criteria: *Lethe* has gotten more troublesome and *Pieris* (or the *Synchloe-Pontia* end of it) less so. It now seems to me that the development of my own taxonomic judgments in these genera illustrates the fact that the BSC is still very useful.

Lethe was listed by Ehrlich among his Group I genera—those in which "the species are quite distinct, and are considered by most workers to present no serious problems." This was perhaps a plausible judgment in

1961, but not for long. In 1966 Harry Clench, and in 1968 Ring Carde and I, perceived the possibility of sibling species concealed in the taxon *Lethe eurydice* Johansson. We all arrived at this notion in the usual way one discovers sibling species—by way of biological, not morphological differences; we observed habitat selection. Later, again in the usual way, we found morphological and color/pattern characters which supported the hypothesis that two species were involved. But these were "weak" characters hitherto unnoticed by taxonomists and which would never in themselves have been interpreted as significant at the species level by a conventional museum worker. Virtually simultaneously, C. F. dos Passos made the same discovery and published the first note on it (dos Passos, 1969). We revised his preliminary taxonomic conclusions in an exhaustive paper (Carde, Shaprio, and Clench, 1970), relying heavily on biological and behavioral data such as those reported in Shapiro and Carde (1970). It is now generally accepted that *Lethe eurydice* and *Lethe appalachia* Chermock are distinct species which are sympatric over the northeastern quarter of the United States and perhaps adjacent Canada, but also have extensive allopatric ranges. As the person most responsible for this, I argue that the significance of the habitat selection practiced by these animals in sympatry could only be made out by an observer trained in and using the BSC, whether consciously or otherwise. I also argue that the application of numerical techniques to a large unsorted collection of both species, prior to their recognition by us, would not have generated any suggestion that anything very interesting was going on.

Later the taxon *Lethe portlandia* Fabricius "fell apart" in the same way (Heitzman and dos Passos, 1974). Here the sympatry is seemingly less extensive and the level of differentiation (species, subspecies, or something inbetween) less clear; but again the discovery of morphological criteria to discriminate among the taxa was contingent on the initial discovery of biological differences in sympatry. Again, I argue, this in turn depended on the mind-set attendant on the BSC. On similar grounds, J. H. Masters has suggested yet a third sibling species may be concealed in "*portlandia.*" Ehrlich, Holm, and Parnell (1974) stated that "investigations of insects, which did not start from the premise that organisms must occur in distinct clusters, have indicated that the ease with which various groups of insects may be fragmented into distinct biological species has indeed been overestimated." Granted a bias—that species do exist in *Lethe*—I cannot see how actual reproductive isolation among natural sympatric populations (subsequently confirmed for *Lethe* by electrophoresis, Angevine and Brussard, 1979) can be interpreted as an artifact of that bias. Historically, the BSC was essential to this study, in a non-circular way.

Lethe in North America went, in less than a decade, from being a staid genus of three "well defined" species (*eurydice, portlandia,* and *creola*

Skinner—I would have thought the last uncomfortably close to *portlandia* to be "well defined" in the Ehrlichian sense!) to being an exciting cluster of five or six or more species arranged in two sibling-species complexes, forcing us to think about why some lineages are prone to speciate with minimal morphological differentiation. Which of Ehrlich's categories fits *Lethe* now? Probably Group 2 ("most species seem distinct, but the status of some forms is in doubt at the present time").

Ehrlich puts *Pieris* in Group 3 ("many or most species present serious problems") because of "the complete confusion regarding the status of the *protodice-occidentalis-calyce-sisymbrii-beckerii* series of forms." (It is plain today that there *is* almost complete confusion in the *napi* Linnaeus group of taxa—Bowden, 1981. The current splitters put *napi* in *Artogeia* and the above list of species variously in *Pontia, Synchloe,* or *Pontieuchloia.*) I frankly have never understood where this "complete confusion" came from though an excellent way to *become* completely confused is to read the only pre-1970 attempt to revise the group, a Master's thesis by W. P. Abbott, part of which was unfortunately published (Abbott, Dillon, and Shrode, 1960); perhaps this disaster was on Ehrlich's mind. The taxa *beckerii* Edw. and *sisymbrii* Bdv. may be removed from the muddle immediately. Both are utterly distinct from each other and from anything else in North America; in fact they are "better species" than most Pieridae and indeed most butterflies. Even Abbott would have excused them from being sunk in his morass of misused mathematics had he ever seen their larvae and pupae!

This leaves *protodice* Bdv. & LeC., *occidentalis* Reakirt, and *calyce* Edwards. Ehrlich is still confused by these in 1981 (P.R.E., *pers. comm.*). Confusion has arisen because there is great phenotypic plasticity, much of which is seasonal and mediated by photoperiodic and temperature influences during development. The control of seasonal and altitudinal phenotypes has now been worked out for a series of geographic populations (Shapiro, 1968, 1973, 1975a,b,c) and the ecological interactions of sympatric populations studied (Shapiro, 1975d). The sexual behavior of both wild animals and caged livestock supports the inferences drawn from environmental experiments, concerning the nature of species in this group. Chang (1963) attempted to justify the distinction between *protodice* and *occidentalis* morphologically. As in *Lethe*, the specific characters are "weak" and unable to stand without strong biological support. We now have that support and can say with considerable confidence that there are two biological species in North America, *protodice* and *occidentalis*; that gene flow between them is a rare, accidental event even when they are abundant in sympatry; and that the taxon *calyce* has been misused in a subspecific sense and should be sunk into infrasubspecific limbo under *occidentalis* (Shapiro, 1976).

On the other hand, study of the Alaskan population, named *nelsoni* by

Edwards, suggests that the proposal by Higgins and Riley (1970)—that *occidentalis* is conspecific with the Palaearctic taxon *callidice* Hbn.—may well be correct. (The same possibility occurred to W. H. Edwards almost a century ago; I am indebted to F. Martin Brown for bringing this non-coincidence to my attention.) Higgins and Riley similarly propose that *P. beckerii* is conspecific with the Palaearctic *P. chloridice* Hbn. This question of conspecificity of allopatric forms is a nagging one, often thrown up by those arguing against the applicability of the BSC in taxonomy (cf. Sokal and Crovello, 1970). We are saved from having to rehash the arguments here by the fact that Ehrlich expressly excluded it from his criteria in classifying the Nearctic genera by ambiguity at the species level. Based solely on the Nearctic fauna, then, I move *Pieris* from Group 3 to Group 1.

I worked on *Pieris* not to redeem it from Abbott or to clear up its taxonomy, but to unravel the history of seasonal adaptation, including polyphenism, in the group. The experimental techniques employed in this regard (reviewed by Shapiro, 1980) can provide good evidence that invasion of severe climates has been accomplished via selection of genes affecting developmental thresholds, but *only* if one assumes that the phylogenetic affinities of the populations can be known. Thus the unraveling of seasonality, and the generation of an historical model with a bearing on a variety of questions from the genetic control of physiological characters to the nature of latitudinal species-diversity gradients, cannot be separated from the unraveling of relationships which become taxonomic when the BSC is employed. Neither makes sense without the other. Obviously the potential multivoltinism/polyphenism of univolting/monophenic populations provides an additional character for numerical taxonomy, but would a pure pheneticist be able to make any biology out of it—if it ever occurred to him to do the experiment at all?

In summary, I maintain that both the increase in number of species recognized in *Lethe*, and the decrease in *Pieris*, were accomplished only because in each case the supposition was made from the start that *there were biological species in these groups*. This is not as circular as it looks. It is presumably possible to arrive at the same conclusions purely phenetically, but not unless the BSC had been used before by field and lab workers since the characters necessary to generate clusters would never have been recognized at all. Ehrlich (1961) says of phenetic classification, "Using such a system it seems obvious that any organisms sufficiently distinct to be sympatric without interbreeding will fall in distinct clusters." Perhaps, but first someone must look for them.

Conclusion

We should be at pains to distinguish between the validity of the BSC as concept or as a mirror of Nature, and its utility in taxonomic practice. I have tried to show that the latter grows out of the former. To me Ehrlich's generic breakdown was merely a demonstration that in a group as thoroughly worked over as the Nearctic butterflies, we are bound to observe the process of transspecific evolution. Ehrlich says (1961): "There are few, if any, groups of equivalent size that are as well-known systematically as the butterflies. Vast collections of them have been amassed. . .the literature is replete with observations on their distribution and. . .their genetics and behavior. If the BSC is usable, it should be easily applicable to. . .the Nearctic butterflies." But this is equivalent, in the context of Ehrlich's argument, to saying that the BSC requires that no evolution occur. Precisely *because* the Nearctic butterflies are so well-known, we should expect them to show many more ambiguities than (say) the bat fleas of Mongolia. The fuzziness of species boundaries is not only predictable from Darwinism; it is an indispensable proof that evolution occurs. If species were well-defined all or even most of the time, neither Darwin nor we would have much reason (beyond pure cussedness) to doubt special creation. The "BSC" demolished by Ehrlich is a caricature, made to appear required to do what it cannot and never could do. Unless we are willing to read evolution out of systematics, the BSC will always be useful in forcing us to think evolutionarily. Whatever one thinks of cladistics, it has reminded many biologists of the importance of the biological species as a unit of evolution and of speciation as a (normally) irrevocable event. The species definition used by Eldredge and Cracraft (1980), though clearly tailored to cladistic specifications, shows a real phylogenetic relationship with Mayr's BSC.

Extremist positions, embraced in the name of consistency, are useful in pointing out problems which we are prone to overlook in everyday practice. As with Aleister Crowley's occult beliefs, quoted at the beginning of this paper, they cease to be entertaining or stimulating once one begins to take them too seriously. The prime virtue of the BSC, and the reason for its survival despite so many withering polemics, has been its ability to generate interesting questions of evolutionary, biogeographic, and systematic interest about real organisms in the real world. In the words of a noted taxonomist: "There seems to be little reason for taxonomists to attempt to reclassify the biosphere numerically, biochemically, or in any other way. For most naming and classifying, the techniques in use today produce special classifications which seem quite adequate" (Ehrlich, 1967).

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